LINKAGE OF CHROMOSOMES CORRELATED WITH REDUCTION IN NUMBERS AMONG THE SPECIES OF A GENUS, ALSO WITHIN A SPECIES OF THE LOCUSTIDAE.

by

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LINKAGE OF CHROMOSOMES CORRELATED WITH REDUCTION IN NUMBERS AMONG THE SPECIES OF A GENUS, ALSO WITHIN A SPECIES OF THE LOCUSTIDÆ.

CARRIE I. WOOLSEY.

In the following paper it is my purpose to give the result of my study of the chromosome numbers within three species of one genus of the Jamaican *Locustidæ*.

The material used was collected in Jamaica during the summer of 1912 by Professor W. R. B. Robertson, of Kansas University. The testes of all but one individual, No. 416, were removed while in the field and fixed in either Bouin's or Flemming's fluid. The slides were made in the fall of 1912. The clearest and best division figures as well as those in which the chromosomes were most crowded together and unsatisfactory were made from Flemming-fixed specimens. The sections were cut at about twelve micra and iron-hematoxylin proved most satisfactory for staining. All drawings have been made at the level of the base of the microscope with the aid of a camera lucida. A 2 mm. Spencer oil immersion lens and No. 18 Zeiss compensating ocular were used. All the figures were magnified to 3,900 diameters and have been reduced 1/5, giving a final magnification of 3,120 diameters.

The specimens studied were identified and classified by Mr. A. N. Caudell of the United States National Museum, Washington, D. C., as follows:

588 and 589, adult males of *Jamaicana flava*, N. Sp., Caudell.

430, a nymph and 560, an adult male of *Jamaicana unicolor*, Brunner.

416, 585, 586, 587, four adult males of *Jamaicana subguttata* Walker.

438, a nymph and 503, a small male of *Jamaicana subguttata*.

In determining the number of chromosomes in the various individuals, I have, in all cases, made drawings from not only different cysts, but from different follicles as well. In a few instances where the figures are particularly clear and distinct, I have taken more than one cell from the same cyst (Nos. 30, 31, 33) but where this was done I made additional drawings from other parts of the testes. There can be no doubt as to the character or appearance of these figures.

Observations.

Jamaicana flava n. sp. Caudell.

All chromosomes are of the rod type. One individual shows two pairs of peculiarly associated chromosomes in the spermatogonial division figures.

In my comparison of species, the description of *J. flava* should logically come first since the chromosomes here are all of the rod shaped, simple type, and are not sufficiently associated to form multiples. They also vary the least in their behavior from what we might consider the original or primitive condition of the species of this genus. To distinguish individuals of the same species, I shall refer to each by number. Nos. 589 and 588 belong to *J. flava*.

In individual 589, I found the number of chromosomes to be thirty-five. They are all rod-shaped, varying in size from the large unpaired accessory chromosome which I have numbered 18, through a graded series of pairs indicated by number, according to their size from 17 to 1.

In a polar view of a spermatogonial metaphase figure, the seventeen or eighteen largest chromosomes are found, as a rule, on the periphery in no fixed position or order, with the smallest pairs clustered about in the center. This is quite well shown in Figs. 3 and 4 while Figs. 1 and 2 show some of the larger chromosomes in the center of the figure where they have probably displaced the smaller ones through some accident in previous mitoses. There seems to be nothing unusual or irregular in the number or relation of chromosomes here either in spermatogonial or spermatocyte divisions.

In the first spermatocyte stages the chromosome complex consists of seventeen undivided autosomes plus the accessory or sex-chromosome (Figs. 10 and 11). As division proceeds, the unpaired sex-chromosome goes entire to one pole accompanied or followed by 17 autosomes. The mates of these seventeen autosomes pass to the opposite pole, thus making the number at the two poles eighteen and seventeen respectively. Before this division takes place, the paired autosomes show the same gradation in size as was noted in spermatogonial figures (Fig. 11). There are several extremely large chromosomes in this individual but the change in the series is so gradual that it is difficult to say where the dividing line falls. However, I am reasonably sure I can pick out at least three pairs in the spermatogonial or three undivided chromosomes in the first spermatocyte cells, that are larger than the others.

In 588, the second individual of *J. flava* studied, a slight but distinct difference can be noted in the spermatogonial figures. The number of chromosomes is the same, thirty-five, and all are of the rod type varying in size as was noted in No. 589. However, in pairing off the chromosomes, I find there are in each cell, two pairs of closely related ones. Each member of the pair No. 16 is always found in close association with a member of the pair No. 14 (*A*, Figs. 5, 6, 7, 8). The members of the other pairs are distributed throughout the figure very much the same as in corresponding figures of No. 589. The largest chromosomes always appear on the periphery and the smallest ones in the center. These two sets of parallel rods, as may be noted, in the figures, have no regular position in respect to each other or to other chromosomes in the cell. Sometimes they are near each other and as often they are to be found on opposite sides of the figure. However, they are never far from the accessory chromosome.

Jamaicana subguttata Walker.

Five individuals out of six belonging to *J. subguttata* show only the rod type of chromosomes. In the sixth individual, a distinct variation is found in the appearance of a V-chromosome.

Of the ten individuals I studied, numbers 416, 585, 586, 587, 438 and 503 belong to *Jamaicana subguttata*. The sections of

No. 416 broke up badly so that it was difficult to find a perfect division figure. However, a sufficient number were found to determine the number and character of the chromosomes (Figs. 13–14).

I found no distinctive feature in the number, arrangement, or behavior of the chromosomes in the first five individuals of this species (Figs. 13 to 29). There are thirty-five chromosomes in each and their appearance is very similar to that noted in individuals, No. 588 and 589. The accessory chromosome is very prominent and in the majority of spermatogonial metaphase figures it is found with seventeen of the largest autosomes on the periphery, the remaining seventeen small ones being in the center of the figure (Figs. 13, 15, 25–29).

A most interesting feature was found however in the individual No. 503. Instead of the thirty-five autosomes of the simple rod type that were common to the other members of the genus as well as species, I found here thirty-three rods and a large V-multiple whose arms are of unequal length. When I attempted to arrange the autosomes in pairs, I found two of the large ones, numbers 16 and 14, without mates among the rod type but corresponding in size to the arms of the V (Figs. 30 to 33). In one cyst I found several perfect cells in spermatogonial metaphase showing this size relation between the rods and the arms of the V (Figs. 30–31–33).

After satisfying myself that this multiple chromosome appears in all spermatogonial metaphase figures, I examined cells in other stages of growth. In the various phases of the first and second spermatocyte cells I found the V still present. In the first spermatocyte figures the rod mates were often still attached to the arms of the V but the break could always be distinguished more or less distinctly (Figs. 37 through 50). In first spermatocyte metaphase (Fig. 42), I found the V still attached to or united with its mates as were several of the rod chromosomes also. In this stage I found fifteen rods without the two in the V and the accessory, making in all eighteen chromosomes in the first spermatocyte.

In the second spermatocyte division the accessory chromosome divides longitudinally so that each daughter cell receives half.

The same kind of division evidently takes place in the V-multiple here. In Fig. 52, we can see the one V going over to one pole a little after the other chromosomes have passed. What appears to be the other half of the V has already reached the opposite pole. I did not find another cell showing this conclusively but the division of the other parts of the chromatin matter would seem to indicate this interpretation. The V at the pole is again the size of the multiple in the spermatogonial stage.

Jamaicana unicolor Brunner.

The two individuals of *J. unicolor* differ. One is of the simple rod type, while the other shows the two V-chromosomes.

The spermatogonial metaphase figures of individual 430.1 show thirty-five chromosomes of the rod type (Figs. 54–57). There is nothing in their appearance or behavior to distinguish them from individual 589 of *J. flava* or from individuals 416, 585, 586, 587 and 438 of *J. subguttata* and the same holds true in later stages of growth.

In No. 560.1, the second individual of this species, I found two multiple chromosomes (Figs. 58–67). In addition to the thirty rod autosomes, the accessory and two large V's are to be seen on the periphery of the spermatogonial metaphase figures. The chromatin material in this series of slides is so badly massed that perfect cells are difficult to find. For this reason I can not be certain of the size relations among all the chromosomes but I have gained the essential facts for my purpose. The largest chromosomes are quite clear and distinct so that I can number the mates of the five largest pairs besides the accessory. Figs. 58–60 show the number and arrangement of the chromosomes. Many spermatogonial cells can be found in which the two V's and the accessory are readily distinguishable although the other chromosomes may be too badly massed for further study (Figs. 61–64).

In the first spermatocyte, the multiples are found attached to each other end to end, thus forming an elongated ring. A slight constriction appears where the ends of the V's meet (Figs. 65–66).

The cells in the earlier growth stages were small and the chromatin so massed together that I gained nothing from them.

Discussion.

McClung and others who have worked on the chromosomes of the *Orthoptera* believe there is a fixed or definite number for each group of related insects, and presumably for all kinds of life. Other writers disagree. Miss Browne ('13) has summarized the work done and results obtained by many investigators on varied kinds of life so thoroughly that I shall not go into this in detail. I shall, however, review the methods as set forth by her whereby the changes in the chromosome numbers have been accounted for by the various authors.

One method is by the fusion or separation of particular chromosomes. Miss Browne in her work on *Notonecta* ('13) and Wilson ('11) on *Nezara* use this explanation. A change in number by a process of fusion was used by McClung ('05) and Robertson ('15) in the appearance of a multiple chromosome, the former in *Hesperotettix* and *Mermiria*, the latter in *Chorthippus* (*Stenobothrus*) *curtipennis*. A change by a process of splitting has been advocated by several observers, Payne ('09) and Wilson ('11) among them. These account for slight or gradual changes but wide variations are accounted for by Wilson by a new segregation of the nuclear material causing a change in number and size relations of the chromosomes, but not in their essential quality. Another method whereby a change might take place is by an abnormality occurring in mitosis. Wilson ('09*a*) has described an unequal distribution of the chromosomes to the daughter cells in *Metapodius*. An arrest of cell division after a division of the chromosomes has taken place was found by Boveri ('05) in sea-urchin eggs.

My material resembles McClung's ('05) in that the change in number is accounted for by the fusion of chromosomes, these giving rise to a multiple (V). However, the composition and behavior of this multiple differs from the one described by him in so far as its relation to the sex chromosome is concerned.

These multiple or V-chromosomes resemble very much more those being described by Robertson ('15) in *Chorthippus* (*Steno*) *bothrus*). Robertson has found that *Chorthippus* (*Stenobothrus-curtipennis* has seventeen chromosomes and of these, six are V's (three pairs of V's). Counting each limb of the V as a chromo-

some, he believes there results twenty-three, the number normal for *Truxalinæ* a subfamily of the *Acrididæ*. It was at his suggestion that I undertook to determine if *Jamaicana* which I found to have these V-shaped chromosomes showed the same phenomena.

In my material the multiple is likewise apparently formed by the union of two of the autosomes. As has been done by others, I numbered and paired the chromosomes according to size, calling the unpaired accessory which is the largest chromosome in the complex, No. 18, and grading the others down from that. I at once found two autosomes of unequal length, No. 16 and 14, without mates as well as the very noticeable V. Since the arms of the V are unequal, and correspond in size as well as length to the unmated rods, I believe No. 16 is the mate of the long arm of the V, while No. 14 mates with the short arm of the multiple (Figs. 30–36). The sex chromosome is very prominent and is often seen in close proximity to the multiple throughout the transitional stages, but it never unites with the components of the multiple as McClung found in *Hesperotettix* and *Mermiria*.

In the spermatogonial metaphase cells the V first appears. It is always on the periphery of the ring with the apex pointing inward, while its rod mates may be anywhere on the periphery, sometimes near it, sometimes opposite it.

From the spermatogonia through the spermatocytes this multiple can be traced. It divides longitudinally in spermatogonia. In the first spermatocyte the tetrads divide transversely separating the V from its rod mates. Half of the second spermatocyte cells receive the V and half receive the rod mates of the V (Figs. 37–47). In the second spermatocyte we have every reason to believe that the V divides longitudinally, each of the two spermatids resulting thus receiving a V while from the other second spermatocyte two spermatids result which will contain the rod mates of the V.

This is what takes place in the one V-type of *J. subguttata*. The associated rods in No. 588 *J. flava* (Figs. 5–8) are easily distinguishable in the polar view of the spermatogonial metaphase and their size 16 and 14 in the series corresponds to that of the arms of the V in No. 503. Their behavior can not be traced as

readily as the V, however, since their union is evidently not permanent and the rods separate in the later growth stages. The fact that they are associated in the early stage forming two sets of related rods on the periphery strengthens my belief in the manner of the V-formation in the other forms. In the place of these two sets of rods, or of the one V and one set of rods in No. 503, I found two V's in No. 560 a representative of *J. unicolor*. Here we find the same thing taking place as in the one V type. In the place of a long V formed by the short V and the rod mates in the spermatocyte figures, we here find a ring formed by an end-to-end union of the arms of the V's (Figs. 65–67).

It will be seen that throughout the three species of this genus of Jamaican *Locustidæ* the number of chromosomes, 35 remains constant, although their behavior varies not only within the genus but even within the species. In seven of the ten individuals studied representing three species, there are 35 chromosomes of the simple rod type. As a whole, the division figures are clear and distinct and the growth stages can be followed with moderate certainty. In the first spermatocyte, the accessory passes undivided to the one pole making the number in the two daughter cells 18 and 17 respectively. When these divide in the second spermatocyte, division takes place longitudinally and the spermatids number 18, 18, 17 and 17 respectively, the last two being without the accessory chromosome. These then will produce males when fused with eggs, and the oosperm will contain thirty-four autosomes plus the one sex chromosome brought in by the egg. Those spermatids with eighteen, will produce females, since here there will be two sex chromosomes, one from the sperm and one from the egg in addition to the thirty-four autosomes, making the number 36 in the females.

I find, however, an exception from this general rule of 35 separate rod type chromosomes in each species studied. *J. flava* shows in one individual the presence of two pairs of associated rods in all spermatogonial figures. The rods that make up each pair or set are unequal and hence can not be mates. In numbering the members of the complex these rank as 16 and 14 in the graded series, 18 being the unpaired accessory and the largest

in the group (Figs. 5–8). I find by numbering the members of the pairs as separate individuals, we have thirty-five chromosomes here as in the other seven forms. In the later stages of growth, nothing appears to distinguish this form from its fellow No. 589 so we must conclude the rods of the related pairs are not held permanently together but are lost after the spermatogonial division among the other rods of the complex.

In *J. subguttata* a multiple chromosome appears resembling a V which I believe has been formed by the union of two of the autosomes. These, by continued association, have finally united end to end and we find them forming a V. The members or arms of the V are unequal and, as was noted in connection with the associated rods, can not be mates, since mates are identical. Hence the mates to the components of the multiple must be rods. I numbered and paired the chromosomes in the spermatogonia according to size and found two rods 16 and 14 without rod mates. These correspond with the arms of the V in size and appearance, and as many cells show the same relation, it seems to me they may be so taken. Figs. 30–36.

The inequality of the parts of the multiple is especially well shown in the first spermatocyte figures. The long arm of the V is linked up with a long rod of approximately the same size, while a somewhat shorter or smaller rod is united with the smaller arm of the V. A slight constriction is to be seen where the rods join the arms of the multiple.

In determining the count for this species, those individuals having the simple rod type chromosomes, have of course thirty-five in their complex. In No. 503, the odd one in this group, there are thirty-three chromosomes of the rod type plus the multiple which I believe is composed of two of these autosome rods united. This then makes the number for the entire species thirty-five, the same as was found for *J. flava*.

The exception in *J. unicolor* contains two multiples or V's similar to the one found in *J. subguttata*. They are apparently formed in the same way and probably of the same two chromosomes, Nos. 16 and 14, as the difference in the lengths of the arms of the V's corresponds with that in No. 503. In the first maturation division, the V's which compose the elongated ring,

break apart at the constriction and each cell receives one V. This splits longitudinally in the next division so that each spermatid carries one V multiple.

J. unicolor contains thirty-one rods and the two multiples. If we accept what has apparently taken place in the previous cases, we can now say the V multiples are composed of four rods which will make the number for the individual thirty-five.

It seems evident then, that the ten individuals, representatives of three distinct species, contain a uniform number of chromosomes regardless of the fact that their behavior differs by the appearance of multiples in two specimens and a transitional form containing associated rods, not yet forming a V, in one individual.

TABULATED RESULTS.

Species.	Accession Number of Specimen Studied.	Number of Free Rod-type Chromosomes.	Number of Groups of Rods Associated by 2's.	Number of V's.	Total Number of Rod Elements (Chromosomes).
J. flava.....	588	31	2	none	35
	589	35	none	none	35
J. subguttata.....	416	35	none	none	35
	438	35	none	none	35
	503	33	none	1	35
	585	35	none	none	35
	586	35	none	none	35
	587	35	none	none	35
J. unicolor.....	430	35	none	none	35
	560	31	none	2	35

Although I made my drawings by the aid of a camera lucida I determined the series of size relations from the slide as well as from the drawing, comparing and judging as accurately as I could the graded pairs. As a result of this study, I believe it is the same 14–16 pair that we find associated in the individuals described, Nos. 588, 503, and 560. Just what significance this may have upon the life processes of these grasshoppers I can not say. As to outer body characters, there is nothing to indicate a variation from those of the simple rod type.

There is still another interesting association in this material that I feel should be noted here. In the cases where a multiple is present, it is more or less closely attended by the extremely large accessory chromosome. In the No. 503 material, this

really occurs more often than my drawings would indicate. Whenever the multiple is seen, whether in an entire cell or only in a section, it is quite rare that the sex chromosome does not accompany it. In the majority of cases, although my drawings do not bear me out in this, spermatogonial figures show these two elements on the same half of the periphery. The No. 560 material shows this particularly well. They are not connected as McClung found in *Mermiria* ('05), and Robertson in *Chorthippus* ('15) but seem to be influenced or attracted by each other so that they are generally found in close proximity.

It seems to me the individuality or genetic continuity of the chromosomes which Wilson ('09) speaks of, is pretty well established here in at least the multiple types. In cysts that show different stages of division, the V may often be distinguished still intact, so that it can be traced from spermatogonia through the second spermatocyte still in the V form. It is quite likely only one half the spermatids of the one-V type receive a V while each spermatid of the two-V type receive one.

I wish to express my thanks and indebtedness to Prof. W. R. B. Robertson for his helpful suggestions and encouragement during the progress of this work.

ZOÖLOGICAL LABORATORY,
KANSAS UNIVERSITY,
September, 1914.

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PLATE I.

Jamaicana flava n. sp. Caudell.

In polar views of spermatogonial metaphase figures, the number of chromosomes in both individuals is thirty-five. Chromosomes are paired and numbered according to size, 18 being the single accessory.

FIGS. 1–4. Polar view of spermatogonial metaphase of individual No. 589.

FIGS. 5–8. Polar view of spermatogonial metaphase of individual No. 588, showing, *A*, the oddly related pairs of chromosomes (14's and 16's) in each figure.

FIG. 9. Lateral view of spermatogonial anaphase. No. 588.

FIG. 10. Polar view, first spermatocyte of individual 589.

FIG. 11. Lateral view of metaphase of first spermatocyte chromosomes numbered according to size. Sex-chromosome going undivided to one pole. Individual 589.

FIG. 12. Prophase of second maturation division or interkinesis.

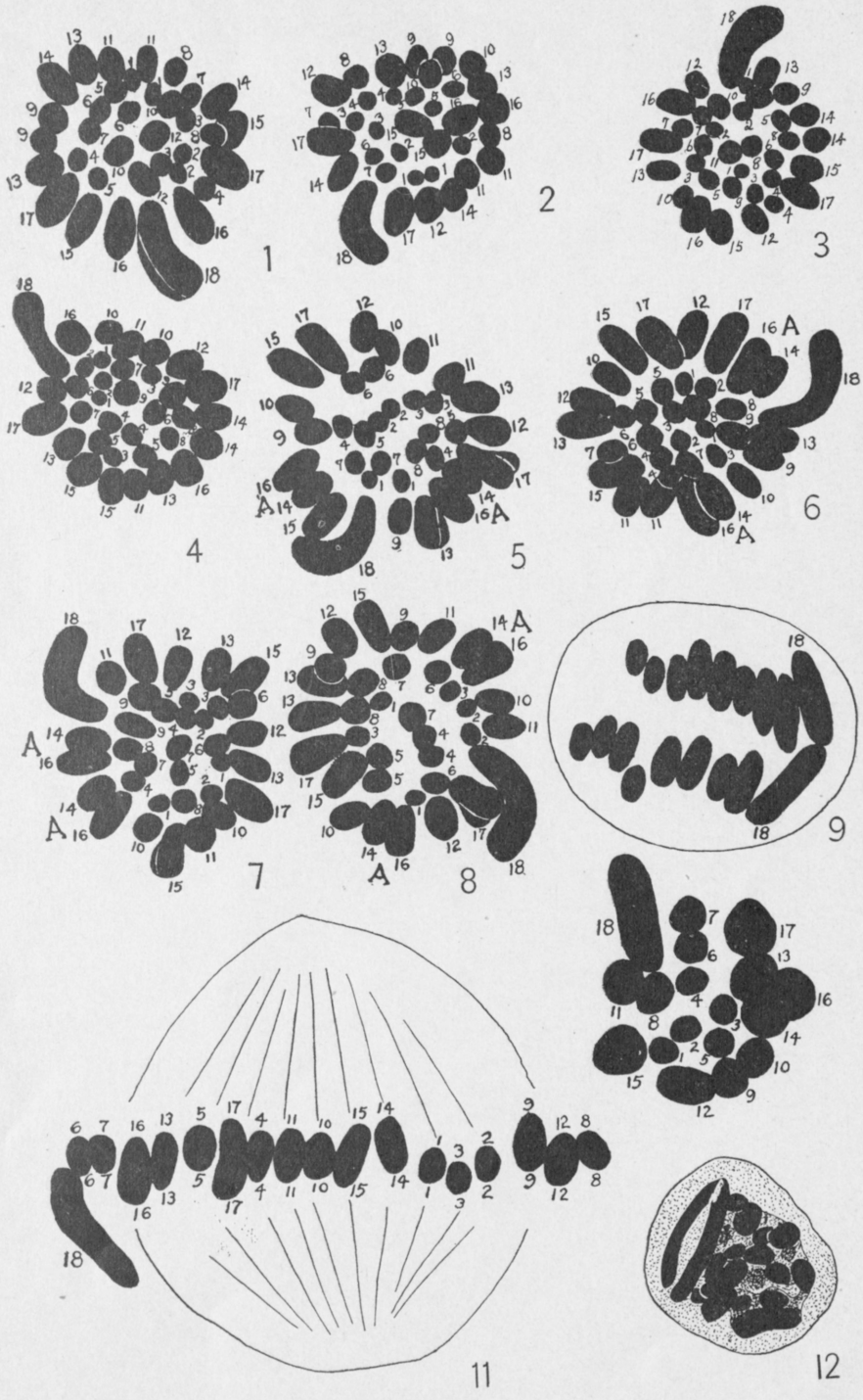
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PLATE II.

Iamaicana subguttata Walker.

Spermatogonial figures from four individuals (Fig. 19 exception). The number in each polar view is thirty-five. Chromosomes are paired and numbered according to size, 18 being the accessory.

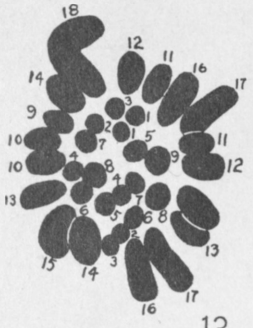
FIGS. 13–14. Spermatogonial figures from individual 416. Polar view, metaphase.

FIGS. 15–18. Polar view of spermatogonial metaphase figures from individual No. 585.

FIG. 19. Lateral view of first spermatocyte. The full number of chromosomes is not shown.

FIGS. 20–22. Polar view of spermatogonial metaphase figures from individual No. 586.

FIGS. 23–26. Polar view of spermatogonial metaphase figures from individual No. 587.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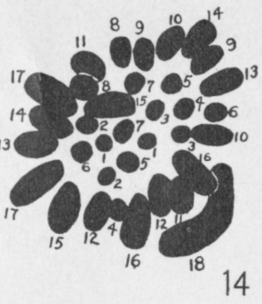
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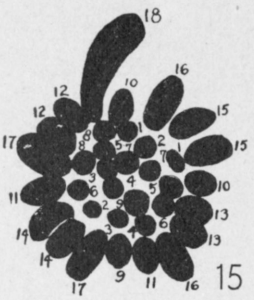
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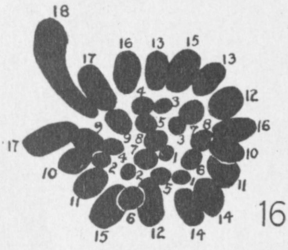
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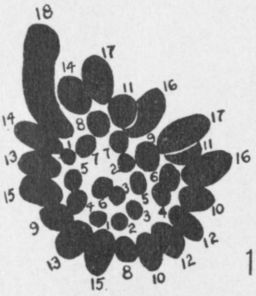
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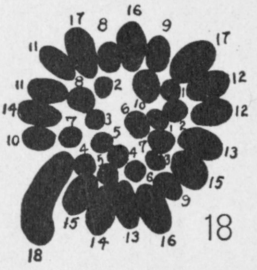
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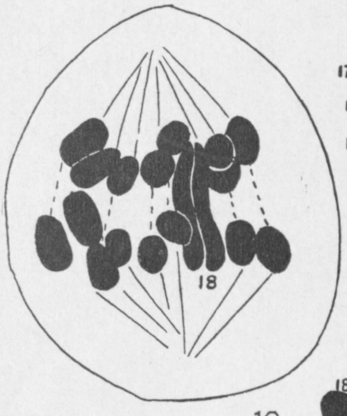
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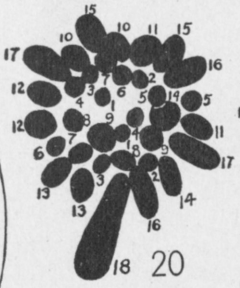
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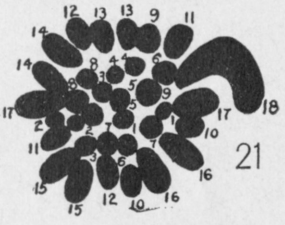
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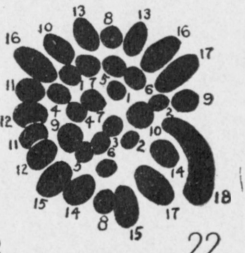
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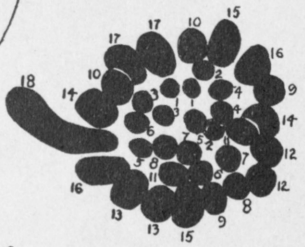
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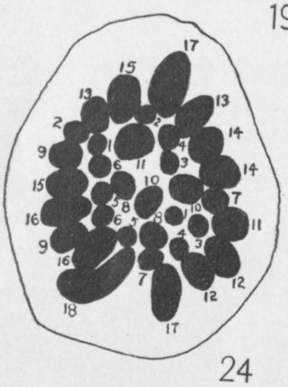
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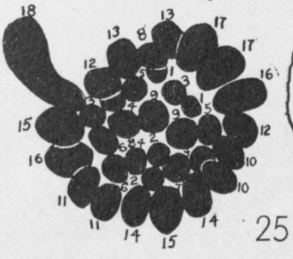
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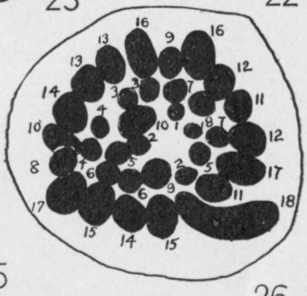
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PLATE III.

Jamaicana subguttata Walker.

Spermatogonial figures from two other individuals of this species. The number of chromosomes in 438, is thirty-five. In 503 there are thirty-three simple chromosomes plus a V-shaped multiple.

FIGS. 27–29. Polar view, metaphase spermatogonial figures of individual No. 438.

FIGS. 30–36. Polar view, metaphase spermatogonial figures of No. 503. The V-multiple chromosome is conspicuous on the periphery.

FIG. 37. First spermatocyte, late prophase showing the long V bi-tetrad of the one-V type.

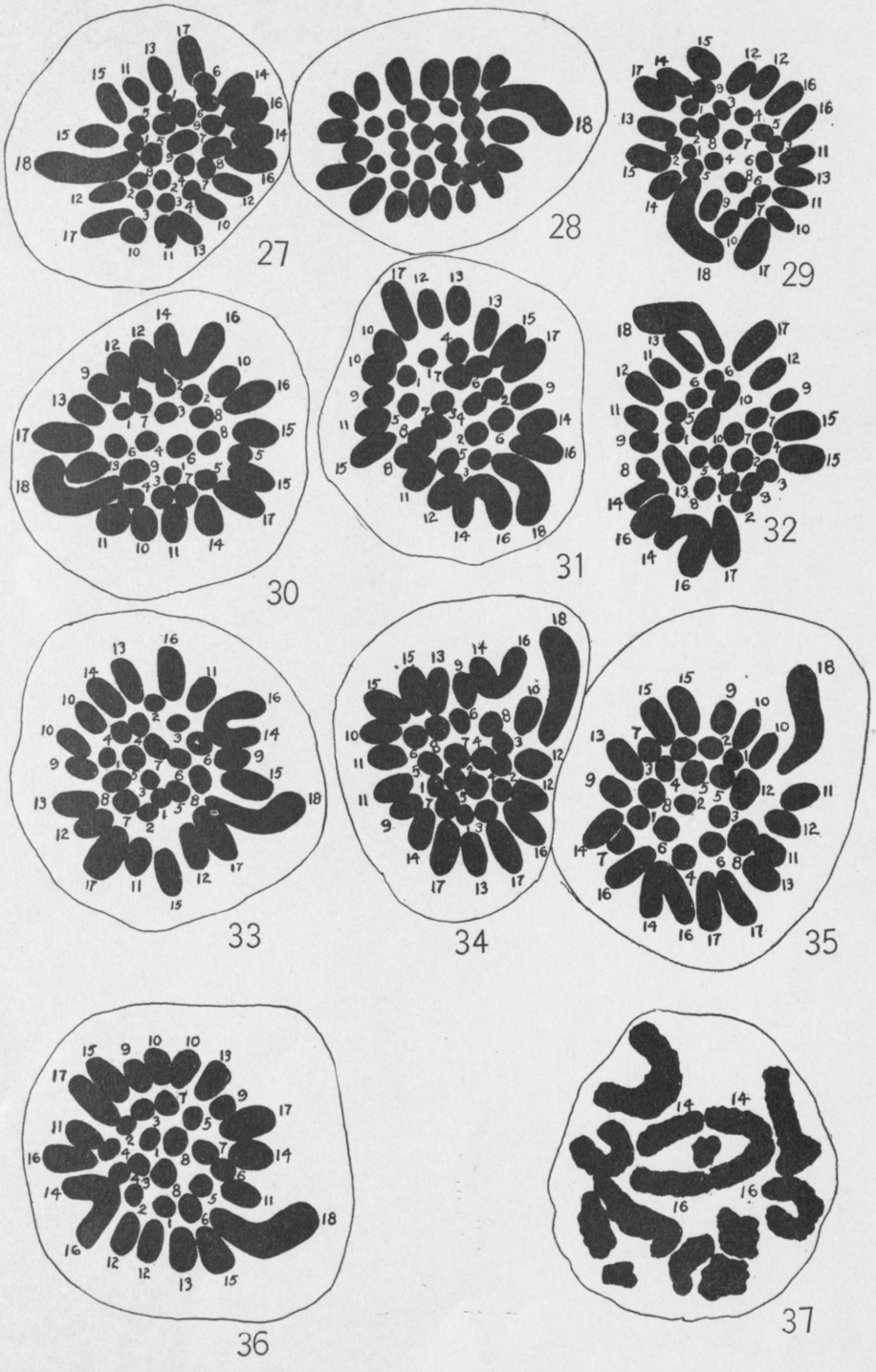
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PLATE IV.

Jamaicana subguttata Walker.

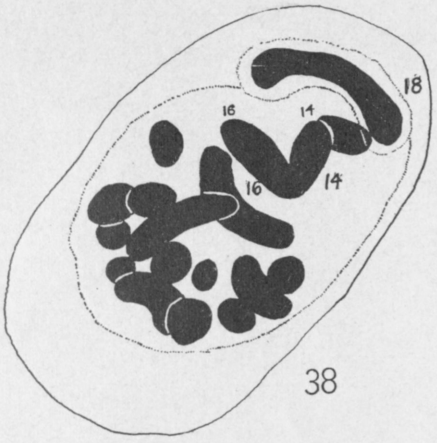
First spermatocyte figures of No. 503.

FIG. 38. Polar view prophase of first spermatocyte showing fifteen simple autosomes, the V-multiple, and the "accessory" chromosome. The latter is enclosed in a receptacle apart from the other chromosomes.

FIGS. 39–41. Lateral view metaphase of first spermatocyte showing the multiple chromosome. The constrictions in the arms of the V show where the rod mates are about to pass to the opposite pole, breaking away from the multiple at the constricted places. The full number is not present but the accessory is prominent in 39 and 40.

FIG. 42. A spermatocyte figure showing the full number, 15, of tetrad chromosomes plus the double tetrad, plus the sex chromosome.

FIG. 43. First spermatocyte showing double tetrad and the accessory chromosome.



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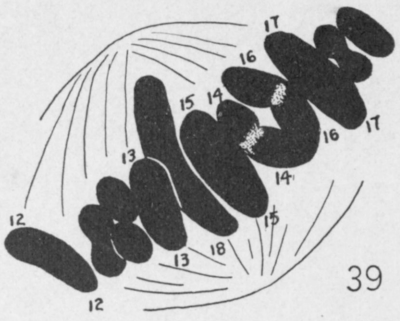

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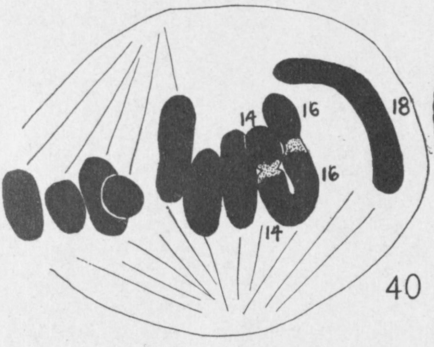

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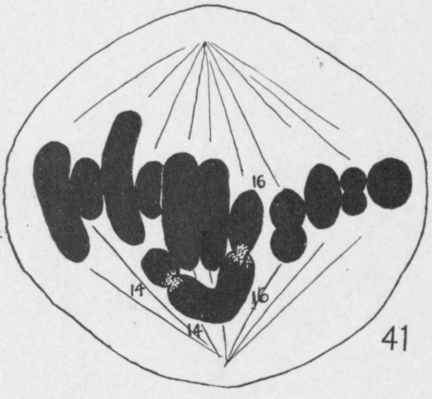

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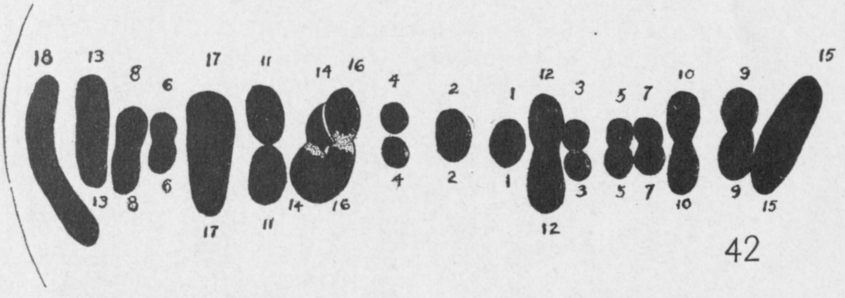

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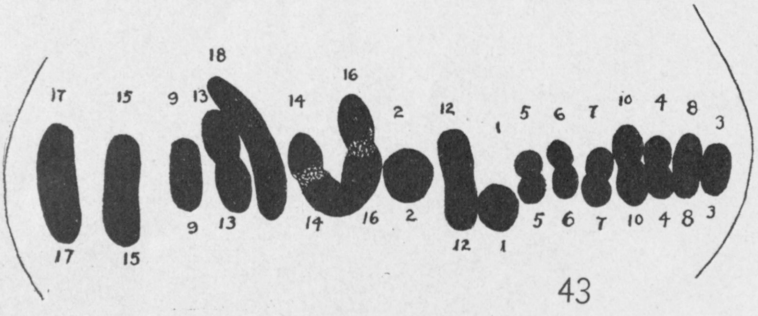

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PLATE V.

Jamaicana subguttata Walker.

Spermatocyte figures of No. 503.

FIGS. 44–46. First spermatocyte anaphase. The multiple chromosome is to be seen in each figure. It has lost its rod mates, which have probably gone to the opposite pole, and is now the size of the spermatogonial V. By comparing it with the multiple before division as seen in Figs. 39–43, what has taken place, is more readily seen.

FIGS. 47. First spermatocyte telophase showing the V at one pole and its rod mates and the sex chromosome at the other. The latter is split longitudinally.

FIG. 48. Telophase of a first spermatocyte division.

FIG. 49. Telophase of first spermatocyte division containing the sex-chromosome and the multiple.

FIGS. 50–51. Telophase of the first spermatocyte or resting period of the second spermatocyte. The sex-chromosome is split preparatory to the second spermatocyte division.

FIG. 52. Second spermatocyte. Sex-chromosome divided. The V-chromosome is here divided and the arms are of the original size seen in the spermatogonial figures.

FIG. 53. Second spermatocyte. Sex-chromosome divided.

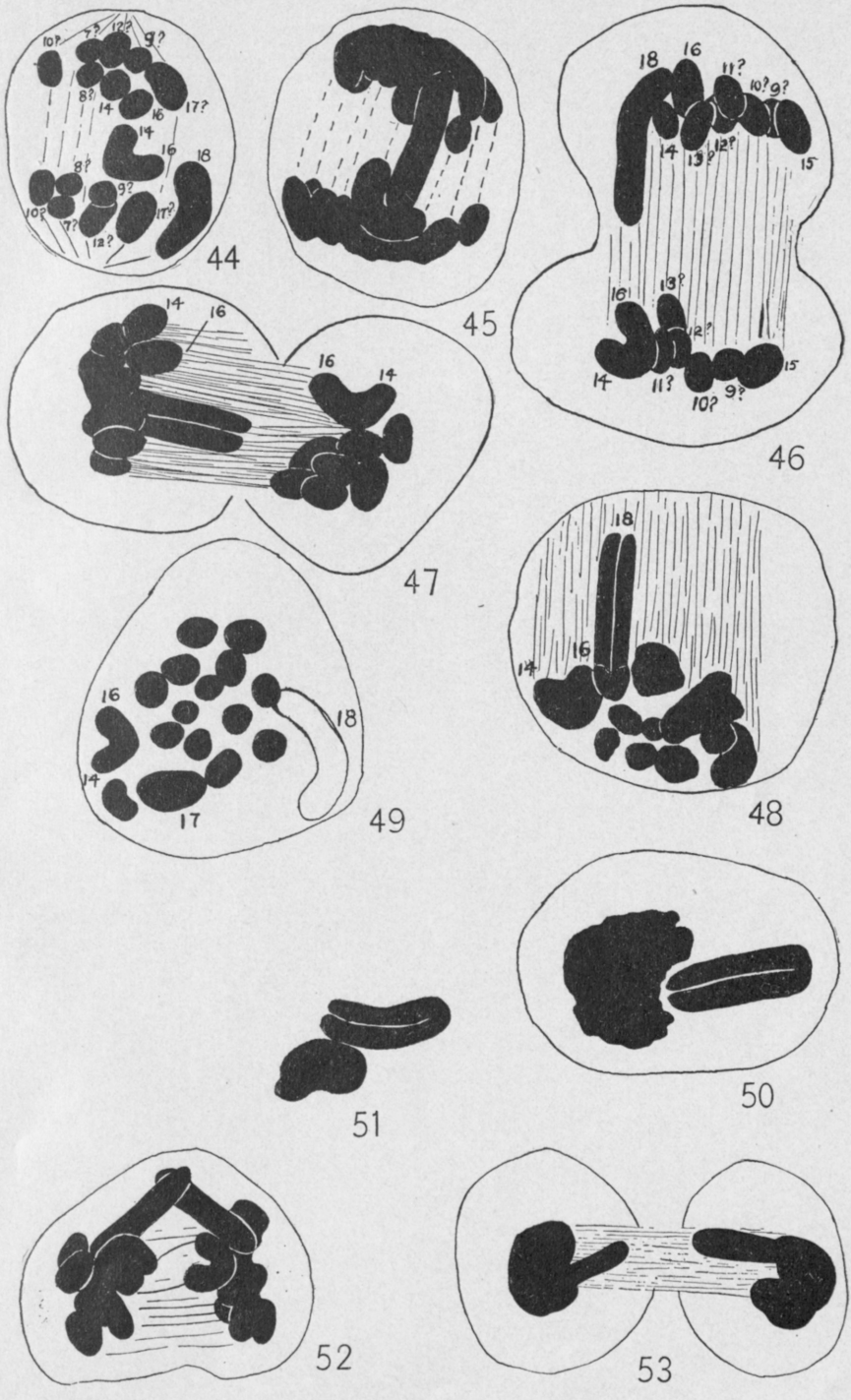
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PLATE VI.

Jamaicana unicolor n. sp. Caudell.

Spermatogonial figures of two members of this species. Thirty-five rods are found in the one; thirty-one rods and two V's are found in the other. Figures 65–67 are first spermatocytes.

FIGS. 54–57. Spermatogonial figures of individual 430. There are thirty-five chromosomes of the rod type here, paired and numbered according to size. No. 18 is the unpaired sex chromosome.

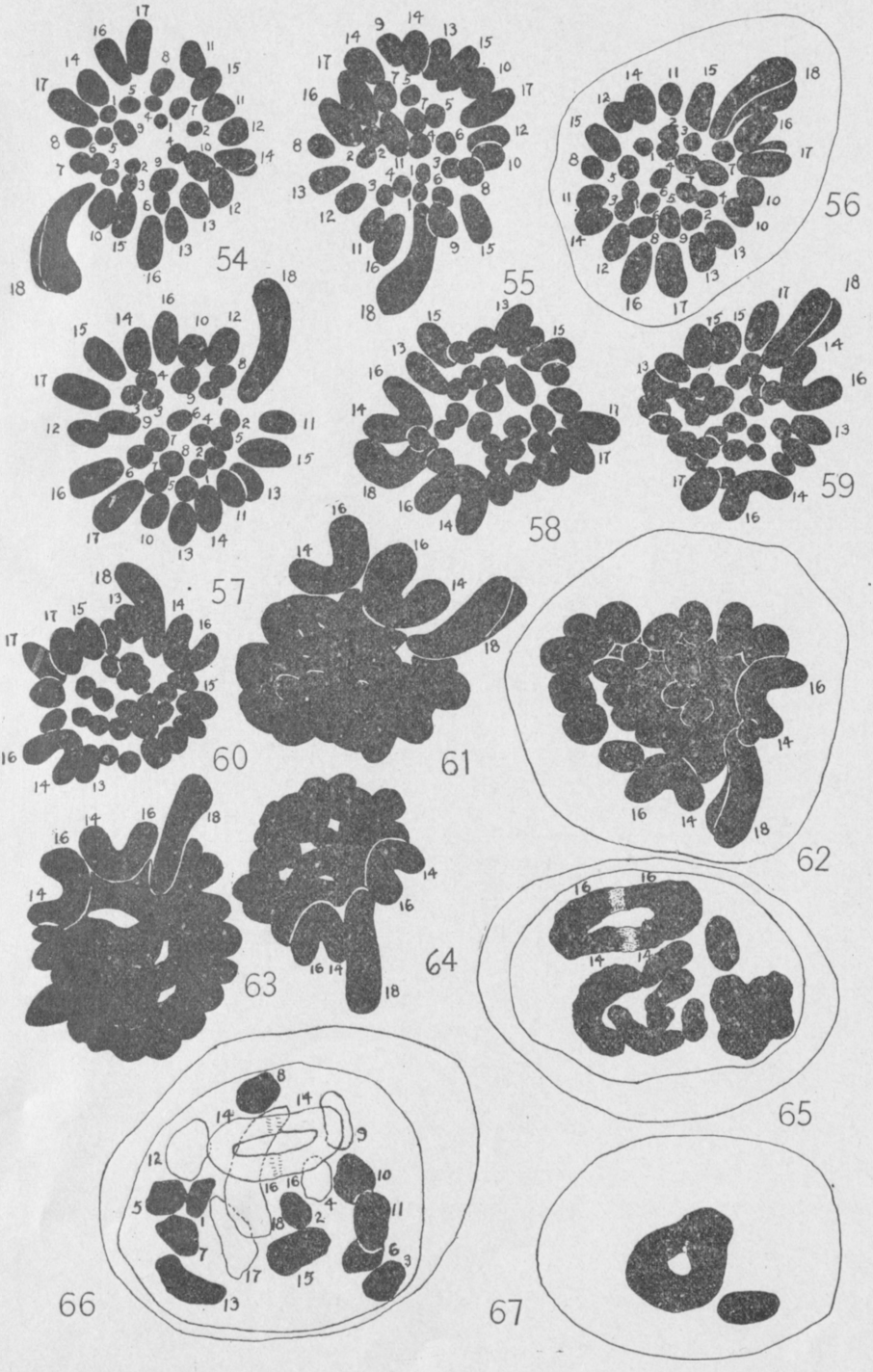
FIGS. 58–60. Spermatogonial figures of individual 560 showing thirty-one rods and two V's in each. No. 18 is the unpaired sex-chromosome. Just the largest chromosomes are paired and numbered.

FIGS. 61–64. Spermatogonial metaphases. Although the chromatin material is much massed, the sex and the two V-chromosomes are very prominent and distinct.

FIG. 65. First spermatocyte of individual 560 showing the multiple or bi-tetrad formed by the two V's.

FIG. 66. First spermatocyte prophase showing the complete number of chromosomes in individual 560,—fifteen rod tetrads, the bi-tetrad, and the sex-chromosome.

FIG. 67. The ring-shaped bi-tetrad more condensed in a latter prophase.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